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UNITED STATES DEPARTMENT OF AGRICULTURE

DEPARTMENT BULLETIN No. 1191

Washington, D. C. ▼ December, 1923

POTASH FROM KELP

EARLY DEVELOPMENT AND GROWTH OF THE GIANT KELP, MACROCYSTIS PYRIFERA

By

R. P. BRANDT, Cooperator of the United States Department of Agriculture

with introduction by

[J. W. TURRENTINE, Scientist in Soil Laboratory Investigations, Bureau of Soils

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POTASH FROM KELP: EARLY DEVELOPMENT AND GROWTH OF THE GIANT KELP, MACROCYSTIS PYRIFERA.

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With Introduction By J. W. TURRENTINE, *Scientist in Soil Laboratory Investigations, Bureau of Soils.*

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INTRODUCTION.

In the paper here presented are results obtained by Dr. R. P. Brandt in two years' study of the life history of the giant kelp, *Macrocystis pyrifera.* The work on which this paper is based was carried on principally at the Scripps Institution for Biological Research under the supervision of Dr. William E. Ritter, director of the institution, and particularly of Prof. W. C. Crandall, business manager and scientist of the institution and likewise a collaborator of the United States Department of Agriculture. The researches here were undertaken as a part of the broader study of the economic utilization of the giant kelps of the Pacific for the manufacture of potash and other chemicals, for which work the Congress of the United States made a number of appropriations, principally for the erection and operation of the experimental kelp-potash plant at Summerland, Calif., as operated by the Bureau of Soils of the United States Department of Agriculture. An active collaboration was maintained between the work carried on by Doctor Brandt at the Scripps Institution and that at Summerland, and the economic phases of his studies were accordingly given emphasis. The unfortunate and tragic death of Doctor Brandt brought his investigations to an immature close. The paper here presented accordingly does not represent an exhaustive research on the subject studied, but nevertheless, conveys so many facts of interest and importance that its

publication is deemed imperative even in its present form. Any further details to be established must be left for future investigators.

While this paper is essentially a study of plants, an activity normally coming within the sphere of the Bureau of Plant Industry, it is published by the Bureau of Soils because it has been through that bureau that the investigation of the economic utilization of the giant kelps has been prosecuted.

Other papers of series.—This paper is offered as a part of a series dealing with the industrial utilization of kelp. Other papers of this series already published are: The Kelps of the United States and Alaska, by William Albert Setchell; Ecological and Economic Notes of Puget Sound Kelps, by George B. Rigg; The Kelps of the Central California Coast, by Frank M. McFarland; The Kelps of the Southern California Coast, by W. C. Crandall; Brief Notes on the Kelps of Alaska, by Edward C. Johnston; The Composition of Kelps and the Technology of the Seaweed Industry, by J. W. Turrentine; A Discussion of the Probable Food Value of Marine Algæ, by Carl L. Alsberg, published as appendices to The Fertilizer Resources of the United States, Senate Document No. 190, Sixty-second Congress, second session, December 18, 1911; Pacific Kelp Beds as a Source of Potassium Salts, by Frank K. Cameron; The Kelp Beds from Lower California to Puget Sound, by W. C. Crandall; The Kelp Beds of Puget Sound, by George B. Rigg; The Kelp Beds of Southeast Alaska, by T. C. Frye; The Kelp Beds of Western Alaska; by George B. Rigg, published as parts of Report No. 100, Potash from Kelp, Bureau of Soils, April 10, 1915; Potash from Kelp: The Experimental Plant of the United States Department of Agriculture. Preliminary Paper, by J. W. Turrentine and Paul S. Shoaff (J. Ind. Eng. Chem. *11*, 864, 1919); Note on the Distillation of Kelp, by J. W. Turrentine (Proc. 8th Internat. Cong. Appld. Chem., *15*, 313); The Experimental Distillation of Kelp at Low Temperatures, and The Preliminary Examination of Kelp Distillates, by G. C. Spencer (J. Ind. Eng. Chem. *12*, 682 and 786, 1920); Continuous Countercurrent Lixiviation of Charred Kelp, by J. W. Turrentine and Paul S. Shoaff (ibid, *13*, 605, 1921); The Applicability of Kelp Char as a Bleaching and Purifying Agent, by J. W. Turrentine and H. G. Tanner (ibid, *14*, 19, 1922); The Decolorizing Action of Adsorptive Charcoals, by H. G. Tanner (ibid, *14*, 441, 1922); The Manufacture of Potash Salts, by J. W. Turrentine, H. G. Tanner, and P. S. Shoaff (ibid, *15*, 159, 1923); Certain Equilibria Used in the Manufacture of Potassium Chloride from Kelp Brines, by J. W. Turrentine and H. G. Tanner (in press).

LIFE HISTORY OF MACROCYSTIS PYRIFERA.

SPORES.

Macrocystis reproduces by means of minute "swarm spores." These are borne on the slender, short-stemmed leaves found densely clustered at the base of the plant. These leaves, or sporophyls (fig. 1), may be deeply grooved or perfectly plane; and the spore-bearing areas, or sori, may be either continuous, completely covering both surfaces, or confined to the grooves. Millions of spores are liberated during a year, by each sporophyl. They are olive green in

color, and differ but little in appearance from the spores of some of the green seaweeds. The diameter varies from about 2 to 6 microns and the length from about 4 to 6 microns; in other words, it would take 200 or 300, placed end to end, to span a pinhead. They vary in form from nearly globular to slender spindle-shaped. The spores borne in the autumn are mostly of the spindle-shaped type, are small, only slightly colored, and highly motile. The large globular spores appear mainly in midwinter. They are deeply colored, very sluggish, and soon come to rest. The cilia by means of which the spores swim can scarcely be distinguished in living spores under the ordinary powers of the microscope, but they are very slender, and attached either at the apex or on the side of a spore.

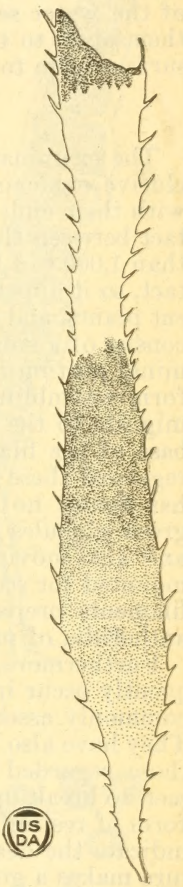

FIG. 1.—Sporophyl. Shaded areas are sori. Remnant of ripe sorus at the tip, young sorus developing at the base and lengthening as leaf grows. One-half life size.

PLANTING IN AQUARIA.

Spores have been repeatedly germinated in the laboratory and the sporelings kept alive for a period, sometimes of several months. For successful germination a cool, well-lighted room is required. A glass vessel is the best container for the culture, on account of its permitting full penetration of light. If it is possible, a constant stream of sea water at ocean temperature should be kept running into the vessel, or if there are not the means for keeping a stream running, the water should be changed frequently and, in addition, should be frequently agitated to work in air. With suitable conditions, sporelings may be had by placing a few fresh, mature sporophyls in the culture vessel. Whether the spores are good or not can quickly be found out by scraping off a little of the soft tissue near the tip of a sporophyl and examining it under the microscope. Healthy spores float out and soon may be seen swarming about in a manner resembling bees. Within an hour after planting the sporophyls the water takes on a brown color as though full of fine mud. This color continues for a day or two, but finally the water clears if there is good circulation. This subsequent clearing is due to many spores coming to rest or attaching themselves to a fixed object. The spores come to rest sometimes in a few minutes; at other times they may swim for 24 hours. Currents have much more to do with their wide dissemination than has their own motility, but the latter probably enables them to get out from the shade of the parent plant.

When the spores come to rest they take on a globular form, and their walls become thick and mucilaginous, enabling them to cling to the glass walls of the culture vessel or to any other object with which they may come in contact. If there is no circulation in the culture vessel, the spores become the prey of bacteria within two

days, no matter what precautions are taken. On the other hand, with good circulation and aeration the walls of the vessel soon take on a rich brown color, especially where the air supply is more plentiful.

The sporelings have slender, club-shaped germ tubes. (Fig. 2, C.) In a healthy culture spores may be found germinating six hours after the planting of the sporophyls. Many spores floating on the surface of the water seem to germinate more slowly, and those that attach themselves to the sides of the vessel within 4 inches or less of the surface seem to grow the best.

EARLY STAGES.

The examination of millions of sporelings has not furnished conclusive evidence of sexuality. Young sporelings have been found with their club-shaped ends in contact, but the cell-wall was still intact between the two plants. They were always outnumbered more than 1,000 to 1 by similarly shaped plants whose tips were not in contact, so it appears to have been a case of chance contact of independent plants, and not of fusion of germ-tubes. The germ-tubes usually consist of a single cell for the first week or two. Gradually the terminal portion increases its diameter until many sporelings assume a form resembling dumb-bells. The color-bodies, or chromatophores, migrate to the enlarged end, leaving the old spore and the slender base of the filament colorless. A number of recent observers have regarded these plants as male or antheridial plants, but the author has found no satisfactory evidence that they are. Minute olive-green globules have often been seen in sporelings 1 or 2 weeks old, and also moving about in the water in which the sporelings were mounted for study, but they have never been seen moving within the filaments preparatory to escaping, as the sperms move within the antheridia of mosses.

Furthermore, these bodies that might be regarded as sperms frequently occur in sporelings that show no thickening. They are also commonly associated with an undivided part of the chromatophore. They have also been seen in plants that differed greatly in form from those regarded as antheridial, and Pelagophycus spores have been seen to break up into such bodies even before assuming the globular form of resting spores. Their occurrence, therefore, seems merely to indicate the death and decay of sporelings. Very commonly a culture makes a good growth for two or three weeks and then suddenly dies out. The spores seem to germinate readily and pass the first stages under conditions not at all favorable for further development.

With good circulation and aeration at a temperature of 14° to 16° C. the sporelings continue to grow for two months or more. The enlarged and condensed ends of the dumb-bell shaped sporelings continue to enlarge and soon begin to divide, by cross walls, to form chains of cells. The color, hitherto olive-green, becomes the characteristic brown of Macrocystis. The filaments may become 5 to 10 cells long and they often branch extensively. (Fig. 2, D.) These may be gametophytes or sexual plants, but none has been found giving rise to leafy kelp plants, nor has a structure been found in one of them that could be identified as an oogonium or egg cell. They seem instead to form various fantastic little plants and then die.

Typical kelp plants, or sporophytes, as they are called by those who believe them to be of sexual origin, arise from what often ap-

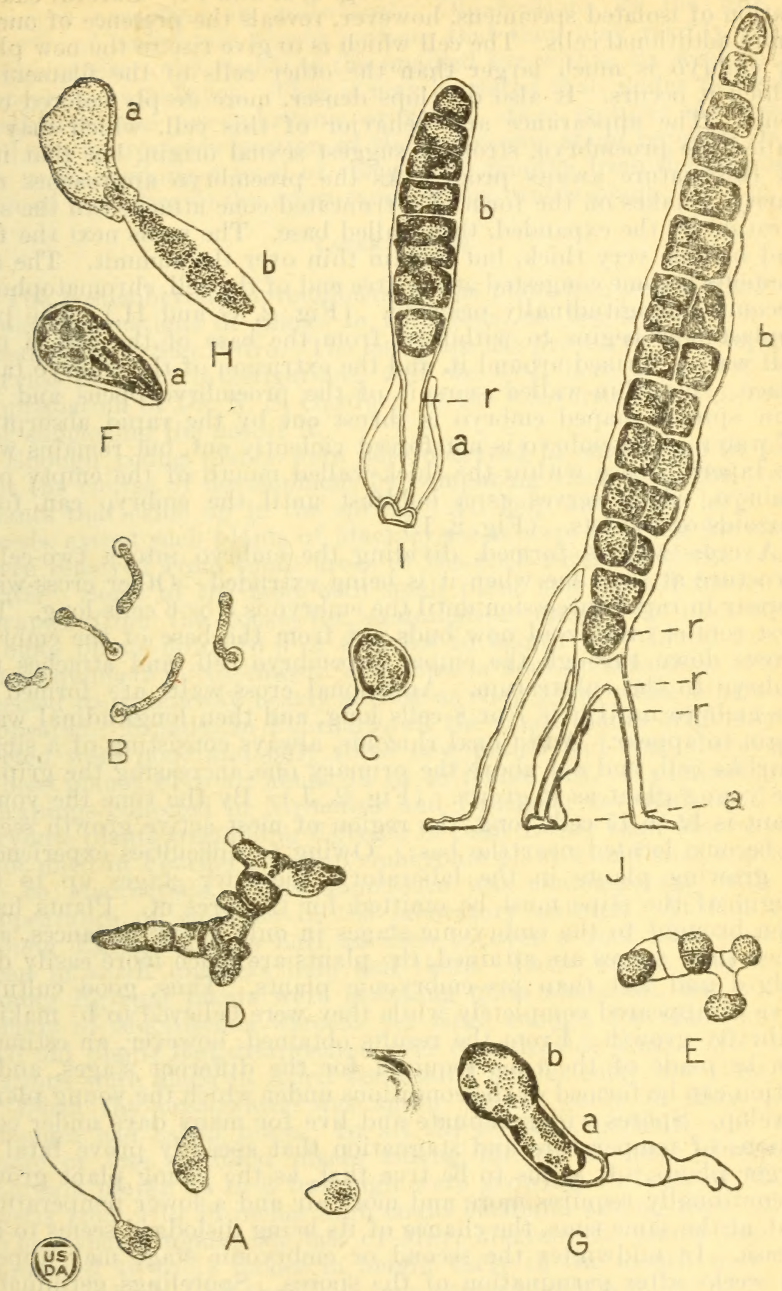

FIG. 2.—*A*.—Spores stained in methylin blue. Drawn with a camera lucida, using a No. 10 eyepiece and a 1-mm. oil-immersion lens. *B* to *J*.—Sporelings in various stages of development. *B* and *G* stained in methylin blue and drawn with a camera lucida, using a No. 10 eyepiece and a 4-mm. dry objective. Remaining drawings reconstructed from sketches of living specimens. *a*=proembryo; *b*=embryo; *r*=rootlets or rhizoids. *A*, more highly magnified.

pear to be single isolated cells. (Fig. 2, E and F.) Careful examination of isolated specimens, however, reveals the presence of one or more additional cells. The cell which is to give rise to the new plant or embryo is much larger than the other cells of the filament in which it occurs. It also develops denser, more deeply colored contents. The appearance and behavior of this cell, which may be called the proembryo, strongly suggest sexual origin, but that it is of this nature awaits proof. As the proembryo approaches maturity, it takes on the form of a truncated cone attached to the substratum by the expanded, thin-walled base. The walls next the free end become very thick, but remain thin over the summit. The cell contents become congested at the free end of the cell, chromatophores becoming longitudinally oriented. (Fig. 2, G and H.) The protoplast now begins to withdraw from the base of the cell, a new cell wall is formed around it, and the extrusion of the embryo takes place. The thin-walled summit of the proembryo opens and the now spindle-shaped embryo is thrust out by the rapid absorption of water. The embryo is not forced violently out, but remains with its tapering base within the thick-walled mouth of the empty proembryo, which serves as a holdfast until the embryo can form rhizoids or rootlets. (Fig. 2, I.)

A cross-wall is formed, dividing the embryo into a two-celled structure at the time when it is being extruded. Other cross-walls appear in rapid succession until the embryo is 5 or 6 cells long. The first rootlet or rhizoid now buds out from the base of the embryo, grows down through the empty proembryo cell, and attaches the embryo to the substratum. Additional cross-walls are formed in the embryo until it is 7 or 8 cells long, and then longitudinal walls begin to appear. Additional rhizoids, always consisting of a single hairlike cell, bud out above the primary one, increasing the grip of the young plant as it grows. (Fig. 2, J.) By the time the young plant is 12 to 15 cells long, the region of most active growth seems to become located near the base. Owing to difficulties experienced in growing plants in the laboratory, the later stages up to the origin of the stipe must be omitted for the present. Plants have been brought to the embryonic stages in only a few instances, and when these stages are attained, the plants are much more easily dislodged and lost than pre-embryonic plants. Thus, good cultures have disappeared completely while they were believed to be making a thrifty growth. From the results obtained, however, an estimate can be made of the time required for the different stages, and a notion can be formed of the conditions under which the young plants develop. Spores will germinate and live for many days under conditions of temperature and stagnation that speedily prove fatal to larger plants. It seems to be true that, as the young plant grows, it continually requires more and more air and a lower temperature, and, at the same time, the chance of its being dislodged seems to increase. In midwinter the second or embryonic stage may appear six weeks after germination of the spores. Sporelings germinated late in winter or in the spring from February to May grow much more slowly than those germinated in December, apparently requiring several months to reach the embryonic stage. The long and, frequently, branching filaments described above occur mostly in summer and autumn, very few plants apparently developing good

embryos excepting in midwinter. Observations on the rate of growth of embryonic plants indicate that they may readily attain sufficient size to be visible to the unaided eye within six weeks after appearing as embryos. Thus it may be stated that, under favorable conditions, the pre-embryonic or sexual stage requires six weeks, and the microscopic portion of the embryonic stage requires about six weeks, making a total of about three months from the germination of the spore to the appearance of the visible plant.

LATER STAGES.

The postembryonic development of the plant has been worked out from observations of plants in kelp beds, on beaches, and on the breakwater at San Pedro. The last place has proved to be of especial service in these investigations, and we wish here to express our appreciation to Dr. N. S. Gardner, of the University of California, for suggesting the use of it.

Enough young plants were here observed to enable one to piece out the course of development by comparing them with the young plants that came up in the spring. All kelp and other large seaweeds, except such plants of Macrocystis as were reserved for study, were removed from small areas of the rock surfaces of the breakwater. Some of the mud with small plant and animal forms was scraped from the rocks for examination under the microscope. Young plants down to 3 or 4 inches in length were found in very small numbers in November. For three or four months some of these seemed to wear away nearly as fast as they grew, while others disappeared. Finally, in February, all the small plants originally selected were gone and only three new plants had been discovered. These plants were all about 16 to 18 inches tall. Examination of scrapings collected in November and December revealed small embryonic plants resembling Egregia in color rather than Macrocystis. Not until in February was an embryonic plant found that appeared to be Macrocystis. This occurrence was contemporary with the appearance of embryos in the laboratory culture. At this time young Egregia plants half an inch to over a foot high could be seen in small numbers here and there. Later on, in March, the young Egregia plants were becoming quite abundant, but no new plants of Macrosystis were as yet large enough for identification. All old plants had disappeared over considerable areas. No observations were made in April because of insufficiently low tides.

When the breakwater was again visited, early in May, great changes had taken place. In all the crevices, pockets, and other more or less sheltered places among the rocks dense clumps of Egregia plants up to 2 feet high were growing. Plants of Macrocystis from 1 to 18 inches high could be found among these others. When visited again, the last of May, Macrocystis plants that had measured 10 to 13 inches in height early in the month were 2 or more feet high. All these vigorous young plants were on rocks that were bare in February and still nearly bare in March. From the evidence furnished by examination of the rocks, microscopic examination of scrapings from the rocks, and experimental cultivation of spores in the laboratory, it seems that young plants of Macrocystis, some of them 18 inches high, had grown from spores ger-

minating not earlier than the previous November and probably not before December or January. Thus a young plant attains a height of 18 inches in the first six months of its life. Very probably under the more favorable conditions of the kelp beds young plants attain a height of from 10 to 15 feet or more in the first six months.

The young plants that had measured 18 inches in height in February had changed so much by the early part of May as to be scarcely recognizable. One not far beyond the end of the first section of the breakwater may be cited as an example. In the middle of February this plant was about 18 inches high, with a slender primary stipe and its first two fronds only well started, a few cysts forming, and the whole plant delicate in appearance. In previous monthly visits, the plant had not been distinguished from the young plants 1 to 6 inches high of the single-bladed kelp, *Laminaria farlowii*, among which it grew. Early in May, less than three months after the plant had been noted as a young plant, with a height of 18 inches, it had a stout primary stipe and main branches, two fronds 5 or 6 feet long—very nearly the length usually attained by plants growing in tide water—with stipes, cysts, and leaf-blades of average size, and 6 additional fronds well started. A considerable number of long, narrow leaves were clustered at the base as in large plants, and on one of these a small sorus was found. When examined under a microscope this sorus was found to have good spore cases, on both sides of the leaf, containing nearly matured spores.

The primary stipe, or "trunk," it may be called, had become stout—over one-half inch in diameter—with a flat holdfast at the base, about 4 inches in diameter, hardly large enough to anchor the plant securely. Six additional whorls of stout hapteres or "roots" were growing out from the stipe above the holdfast. When visited again at the end of the month, the plant had nine good fronds, of which the first two were in the sloughing stage. No fruit was seen, probably because there is a great decline in fruitage in May. All the young hapteres noted the first of the month had grown down and attached themselves to the rock, so that the plant now had a good, stout holdfast, of the conical or dome-shaped type characteristic of large kelp plants of various species. The primary stipe was now starting out from the underside of one of the larger branches.

Working backward from this plant, it may be stated that from the time a young plant has begun to send up its first fronds, not more than four months elapse, if conditions are favorable, until it has produced a clump of fronds of average weight. Then, since plants germinating from the spore in December are sending up their first fronds in May, we can safely say that plants germinating at a time favorable for most rapid development may be producing kelp in commercial quantities in 10 months or less. It is necessary to use the expression, "a time favorable for most rapid development," because, thus far, only spores germinated in early winter have been found to produce rapidly developing plants. Spores germinating even as early as February, when the water is at its lowest temperature, produce sporelings which, while they take on a healthy color, seem to keep their original size for months.

Kelp beds torn out by storms in late winter or early spring do not come back until the second season. This discrepancy between the rate of regeneration of beds destroyed by winter or spring storms

and those dying in the summer is accounted for by the fact that plants from autumn spores develop rapidly, whereas those from late-winter or early-spring spores make little or no progress at first. Thus, in either case, the bulk of the new growth must make its start in autumn or early winter.

The San Pedro breakwater has also furnished interesting data regarding phenomena of development of young plants. They start first in crevices or small cavities where they are not exposed to the full wash of the surf. On the more fully exposed surfaces regeneration is very slow. The plants that do grow up in exposed situations make a much slower growth than those better protected. Protection from violent wave action has much the same effect on the general appearance of a kelp plant as shading and protection from wind have on a land plant: that is, the protected plant produces a longer stipe and much larger, and thinner blades than the exposed plant. Plants in exposed places on the breakwater were not more than 1 or 2 inches high when the better protected plants had a height of 16 to 18 inches. Kelps took hold more readily where the rocks were covered with barnacles and other small animals, and small seaweeds, than where their surfaces were clean. Frequently kelp plants were found attached to small red seaweeds. Where conditions are favorable, the young plants start thickly, often standing less than an inch apart, the strong ones crowding out the weak as they grow.

DEVELOPMENT OF HOLDFAST.

Another very important point observed was the rate of development of the holdfast. The first few whorls of hapteres grow out at very short intervals to form a flat holdfast. This holdfast does not keep pace with the upper parts of a vigorous young plant, and as a result the plant becomes very insecurely anchored. Later on, however, when the primary stipe has become stouter and a number of fronds have been sent up, numerous stout hapteres bud out higher up and securely anchor the plant.

REGROWTH.

A plant selected for regeneration experiments behaved in a manner resembling new plants, as regards seasonal growth. This plant was in a slightly protected place, and was a strong specimen with a somewhat larger holdfast than most of the plants on the breakwater had. The fronds were all cut down to a height of 16 to 18 inches in November. Some new fronds were found growing up in December. These began to weather down when 3 or 4 feet long. New fronds appeared from time to time, but wore back too rapidly to produce much foliage during winter. When visited early in May, there were 12 fronds. None of these was more than 7 or 8 feet long. On some fronds, 3 or 4 feet long and growing vigorously, the lower laterals had already formed clusters of four or more leaves each. All fronds found at this time were cut off below the lowermost cyst. By the end of May, 6 new fronds had started, of which the longest had a length of 3 feet. During the seven months that it was under observation, the holdfast of this plant had increased from about 1 foot to 2 feet in diameter, and had died in the center, showing that the plant has a tendency to spread at the base after

the manner of a clump of mint. This spreading habit of one type of Macrocystis will be referred to later in this bulletin. Many of the basal leaves of this specimen fruited in midwinter, but no fruit was seen in May.

YOUNG PLANTS.

In addition to the observations at San Pedro, careful watch for young plants was kept in various kelp beds and on several beaches. Plants with only one or two fronds, and these with rather slender stipes, thin-walled cysts, and rather delicate leaves such as one would naturally expect young plants to have, are rarely seen in kelp beds. No changes take place in the appearance of a kelp bed by which one can recognize the coming in of a new generation.

At more or less irregular periods, but chiefly in spring and early summer, young plants come in on the beaches in fairly large numbers, though not at all comparably to the young Nereocystis plants that come in on northern California beaches in midsummer. In May, 1919, these young plants appeared in greater number on the beach at La Jolla than at any other time or place considered in this bulletin. Many of these could be readily untangled, and were sufficiently well preserved for measurement. About 400 of these plants were collected and measured for the purpose of finding the rate of growth. The work was discontinued because many young plants of considerable size were soon found that could not be untangled from the masses of seaweed without breaking, but which would have had to be used in order to get results of real value. During May more than 400 plants were measured, having an average length of 3 feet. These regularly had 2 fronds, 2 narrow leaves between the fronds, a slender primary stipe about 4 inches long, and a flat holdfast about 2 inches wide. The development of the holdfast and the size of other parts indicated that they had grown at four or five times the rate of the plants observed at San Pedro.

In addition to these plants, there were others measuring 15 to 20 feet in length. These had their third and fourth fronds well started and the holdfast better developed than in the young plants, but were apparently not more than 7 or 8 months old. On the other hand, very small plants were often found. Some of these were attached to the holdfast of larger young plants, or had grown up so close beside them as to let go and drift ashore with them. Other examples were found of young plants having started on old stems of seaweeds, which had broken off and come ashore with them. One old stipe, apparently Egregia, less than 2 feet long, had more than a dozen young plants attached to it. The smallest plants thus were only 0.2 inch long. These had already formed a stipe, but there appeared to be but little expansion at the base. The blade was very thin and perfectly plane, with a smooth, entire margin. These tiny plants all had the tip more or less worn off. Macrocystis plants can hardly be distinguished from Egregia or other young kelps, especially when they come in with most of their color faded out. Among the drift plants they were regarded as Macrocystis because of having come from too great a depth for shore kelps. On San Pedro breakwater it is not easy to identify Macrocystis before the grooves for the first split begin to appear, because of the great quantity of

shore kelp of which two species, *Laminaria farlowii* and *Eisenia arborea*, also have corrugated leaf blades.

Young plants 3 or 4 feet long were found in some number on the beach at La Jolla in November, 1917. One or two small plants were found among these. Again, in February, 1918, a very few small plants were found, of which two were undivided. In July, 1918, young plants from 1 to 12 feet long came in, in numbers comparable to the smaller plants found in May, 1919. It would thus seem from these observations that young plants may be found at nearly any time of the year, but in abundance only from late spring to midsummer. Plants brought in by storms in winter or early spring usually have large fronds and well-developed holdfasts a foot or more in diameter. Of the other plants, the holdfasts are commonly dead in the center, some having only a shell of living hapteres around the outside. The center begins to die, apparently, in the second year, so that these plants are more than a year old. Some of the largest may be 5 years old or older. The comparatively small number of plants that come in on the beaches certainly indicates a smaller amount of renewal than occurs in a bed of annual kelp. It is not possible, though, to make any near estimate of the age attained. Most plants are probably destroyed by being torn from their anchorage and carried ashore.

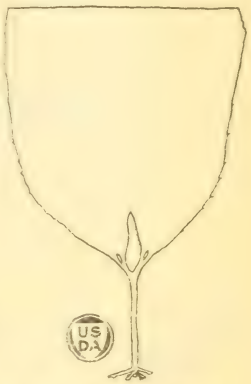

FIG. 3. Lower part of a still larger plant with the primary split well developed and the secondary splits visible at each side. One-half life size.

STAGES OF DEVELOPMENT.

The stages in the development of the plant, after it has become of sufficient size to be seen without the microscope, may be rather hastily sketched, since Skottsberg (*8*)[1] has described them in detail. In the earliest stages thus found, the plant has a single leaf with a broadly rounded base (fig. 3), a distinct stipe, and a conical holdfast. As it grows, hapteres bud out in whorls above the original holdfast. The increase in the length and the diameter of hapteres is very rapid at first. The stipe enlarges upward as successive whorls of hapteres are given off. The intervals between the first few whorls are so short, and the increase in length of successive hapteres so rapid, that the holdfast of a young plant becomes very flat. When a rapidly growing plant has attained a height of 4 or 5 inches, the first longitudinal split begins to develop at the base of the leaf-blade. A vigorous plant may have a height of nearly 2 feet before the right and left halves of the primary blade are fully separated. By the time the first split has attained a length of 1 inch, the secondary splits begin to occur. In contradiction to what Skottsberg (*8*) states, the first splitting usually separates a symmetrical blade into equal divisions. The secondary splits separate the first two leaves into unequal parts, of which the outer or marginal two are larger than the inner or central pair. The margins begin to

[1] Figures in italics in parentheses refer to literature cited at the end of this bulletin.

thicken and lengthen below, giving rise to the two main arms or branches. The outer segments begin to outgrow the inner pair, and very soon the serial splits begin to appear, showing their evolution into the growing tips of the first two ascending fronds. In some plants all the leaves are still attached at their tips to the original blade, even after the first cysts have begun to round up. The characteristic marginal teeth do not appear before the plant has attained a height of 5 or 6 inches. A few teeth then appear below the middle of the blade, but none on the thickened margin at the base, from which the stipe is derived. A growing tip regularly has a few teeth on its outer margin. (Fig. 4.) Teeth appear on the margins of the first cleft when it has attained a length of a little more than an inch, becoming more conspicuous as the plant approaches maturity, developing to their full extent in plants producing stipes and leaves of full weight. In large plants they are longer, more widely spaced, and turn out more sharply from the margins on basal sporophyls than on floating leaves. None occur on the inner margin of a growing tip or terminal leaf of a frond, since this is being continually torn away bit by bit as laterals are given off.

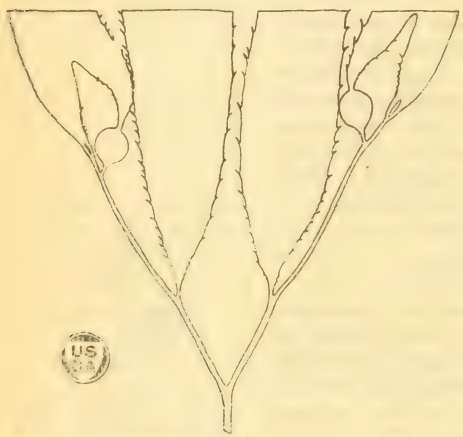

FIG. 4.—Middle portion of a plant 5 or 6 months old. The first pair of fronds beginning to rise from the marginal divisions of the primary blade. The two short-stemmed leaves in the center will both split longitudinally. Of the four leaves thus arising the central two will develop the second pair of fronds.

BRANCHING.

The primary stipe seldom attains a length of more than 5 inches. The first arms attain a length of from 2 to 4 inches and stand out horizontally or curve upward. The next interval, between the second branching and the first leaf on the ascending frond, is sometimes very long, as much as 3 feet in some plants. This first lateral on the frond is provided with a cyst at its base, indicating that the next frond must come from the central pair of leaves, originating at the time of the second splitting, since cysted leaves do not give rise to fronds, and since fronds or leaves do not originate except by the splitting of leaves. When the first two fronds have become well started, the central leaves each split symmetrically, and of the four leaves thus produced, the central two give rise to fronds. There are thus two steps which may be noted in the origin of a frond. The first is the splitting of a basal leaf into two nearly equal divisions. The second is the transformation of one of these leaves into the terminal leaf of a frond. (Fig. 5.) The plant thus always provides a leaf from which another frond may arise. Successive fronds arise from alternate sides of this basal leaf. We should, therefore, expect an old plant to have a short, upright trunk, giving rise to two arms zigzagging upward and sending up a frond at each angle.

Such a plant would send up successive pairs of fronds. The size attained by some kelp plants indicates that they do have that simple method of growing, although the kelp beds are built up by plants of somewhat different habit.

THREE TYPES OF DEVELOPMENT.

After the first pair of fronds make their start, young plants of Macrocystis begin to show differences in the method of development which become more and more pronounced the older the plants become. The different types fall readily into three groups, which may later be separated into distinct species.

The first type may possibly have the simple habit of growth suggested above. It is never a large plant. Usually it occurs in a kelp bed as two or three fronds in a clump differing conspicuously from the remaining fronds. The characteristics are: Slender stipes, large globular cysts with solid, stipe-like bases, and very long, thin leaf blades. Crandall (3) noted the type at Johnson's Lee, Santa Rosa Island, and at Anacapa Island. The author noticed it particularly at the eastern end of San Nicolas Island. The presence of these fronds among those of normal type merely indicates that there are two or more plants in one clump—a very common occurrence. In this case, however, a distinct type is seen to be present whose peculiarities are not due to environment. It has not been the purpose, in these investigations, which have been carried on for practical instead of purely scientific purposes, to try to make species.

FIG. 5.—Terminal blade or "bud" of a vigorous frond. A large number of slender young laterals are partly split off from it. One-half life size.

In the much more common type of Macrocystis, the typical *M. pyrifera*, the second pair of fronds usually bear one or two lateral leaves without cysts at first, cysts appearing later. These may give rise to fronds. There is thus an increase in the number of points from which fronds may arise. Practically all later fronds give rise to additional growing points in this way. Sometimes one of the first fronds gives rise to an additional growing point. Hence, a large plant may eventually be able to send up 20 or more fronds at the same time. The lower portion of such a plant becomes a dense shrub with a few stout, tortuous main stems having numerous branches, which themselves branch extensively. Finally, all the branches change to the slender, cordlike stipes of the floating fronds. These lower stems are harder and tougher than the long stipes. In many, if not the majority of plants, at least some of these basal leaves divide repeatedly without sending up fronds, but give rise instead to dense clusters of short-stemmed leaves. As the plant grows older these bear spores.

The smallest drift plant found bearing spores was 15 feet long. It had apparently come from shallow water, and was, therefore, short for the age which its appearance indicated—about 8 months. Plants do not fruit, apparently, until 9 or 10 months old, and then

only very sparingly, fruitage increasing with age. While the first fronds are growing up and additional fronds and growing points are arising, there is an increase in size in all parts of the plant. By the time the fronds have attained the surface of the water they are producing stipes, cysts, and leaves of nearly normal weight. The basal leaves are as large as those of an old plant. The primary stipe, less than one-eighth inch in diameter in a plant 6 months old, sending up its first fronds, attains a diameter of one-half inch by the time the plant is 9 or 10 months old. As the foliage of the plant becomes heavy and the waves threaten to tear it loose from its anchorage, additional hapteres bud out in three or four whorls at a time. Branching repeatedly, they soon form a dense tangle. These later hapteres are much stouter than those comprising the holdfast of a small plant. The whorls come out at intervals of nearly half an inch. They are produced in such numbers that they soon conceal the primary stipe. Additional hapteres grow down from the branches until an old plant has all the older portions of its lower stems hidden in a huge conical holdfast, sometimes 3 or 4 feet in diameter and more than a foot high. The older hapteres, as well as the portions of stem that bore them, die and decay, so that an old clump has a number of stems bearing fronds and hapteres. It thus becomes impossible to determine whether a large clump has been derived from one original plant or from several. About the time branches begin to send down hapteres, the plants begin to show the differences which separate them into the second and third groups.

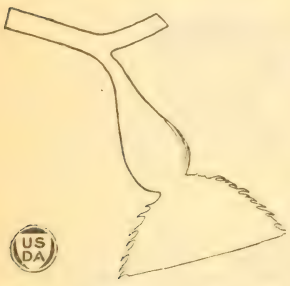

FIG. 6.—Small upper part of stipe, showing ordinary form.

In the second group the shrubby lower stems ascend more or less steeply from the base. They grow upward much more rapidly than successive whorls of hapteres ascend them, thereby attaining a height of a foot or more above the top of the holdfast. Because of rather slow growth and ascending habit, the group of stems or axes remains centrally located, and the larger the holdfast becomes the longer the hapteres have to be to take hold around the outer edge. The increasing difficulty of producing hapteres of sufficient length to secure it to its anchorage is one of the factors determining the length of life attained by the plant. This is the typical *Macrocystis pyrifera*, with the typical pear-shaped cysts, hollow nearly to the base—the most abundant deep-water type on the southern California coast.

It is often greatly modified by environment. In the more exposed beds of the islands, the stipes are very stout, the cysts long and tapering, with thick walls, and the blades long, narrow, and very thick. The plants are tough in texture, and rich chestnut brown in color. In the quiet water of the more sheltered island harbors the plants have slender stipes, nearly globular thin-walled cysts, and very broad, thin leaves, sometimes more or less heart-shaped at the base. The color of the whole plant is pale yellowish brown, and its leaves are very fragile. Along the mainland the plants are inter-

mediate between the two types, sometimes grading more or less into the latter. Figures 6, 7, and 8 show these environmental types.

In the third type the branches assume a horizontal position and send down numerous hapteres from the lower side. These creeping stems or "rhizomes" spread from rock to rock, rooting nearly to the tip, and thereby anchoring themselves very firmly, but are never centrally located. The fronds rise from around the edges of such a clump. The hapteres never have to grow far to reach their support if the plant is growing on a suitable bottom. As the center dies out, branches of the rhizomes grow in to take its place. When torn up by storms, this type comes ashore with pieces of the holdfast 1 or 2 feet in diameter. Theoretically its life and the extent to which it may spread are unlimited. It appears to produce a shorter frond, with smaller leaves, than the typical *M. pyrifera*, but because of the immense number of fronds sent up it makes a very heavy mat. This type has been found all along the southern coast, but in greatest abundance near Redondo. It seems to affect shallower water than the other forms, and probably is an important component of the kelp beds that are most heavily matted toward shore.

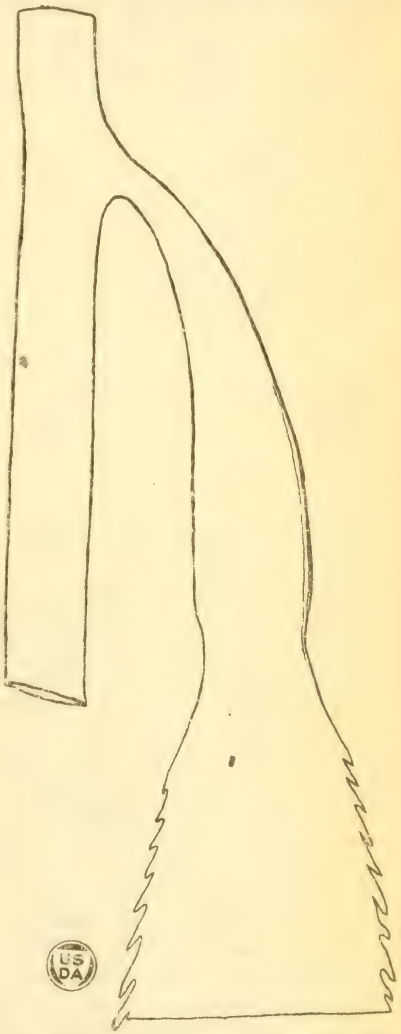

FIG. 7.—Rough-water form: cyst and stipe parallel.

There is no recognizable difference between the floating parts of this plant and those of the typical *M. pyrifera*. The rhizome-forming type is especially well exemplified by the shore Macrocystis found in or just below tidewater on the coast of central or northern California, a clump of which, apparently from one original plant, may cover every bowlder over a space 50 feet wide and may persist for many years. Its fronds are short, 15 to 30 feet, its rhizomes are over an inch wide, flat, and sharply differentiated from the ascending stipes. The most violent storms seem able to tear off only small fragments of it, and a patch completely stripped of fronds in winter usually renews itself the following summer.

SIZE ATTAINED.

Plants in 50 feet of water at La Jolla have been found with fronds floating on the surface a distance of 70 feet. If these plants were attached to the bottom, they therefore had a length of 120 feet. The majority of plants in the same locality do not apparently reach a length of more than 100 feet. In 20 or 25 feet of water plants attain a length of 30 or 40 feet, and where they have been found growing in tidewater on the coast of southern California they seldom attain a length of more than 10 feet. The most vigorous specimens found were at San Nicolas. They appeared to float on the surface for about 100 feet and may have had a total length of 150 feet. The longest leaves found at San Nicolas measured nearly 6 feet, but were only 4 inches wide. These were on plants of the first or very slender type; they were attached to globular cysts nearly 1½ inches in diameter. Plants of the typical *M. pyrifera* associated with them had leaves as long as 5 feet, cysts 3 or 4 inches long, and mostly about 1 inch wide, and stipes about one-third inch thick. The leaves averaged 36 inches long by 3 inches wide. Plants of *M. pyrifera* have been found there with leaves 50 by 7 inches, cysts 4 to 6 inches long and sometimes 1½ inches wide, and stipes one-half inch thick. At Santa Barbara Island leaves of the quiet-water form have been found which measured 50 by 10 inches. These were attached to cysts about 2½ inches long and 1¼ inches wide, on stipes one-fourth inch thick. At La Jolla and other mainland beds leaves are usually 18 by 30 inches long and 4 to 6 inches wide, cysts 2 inches by five-eighths inch, and stipes slightly more than one-fourth inch thick. Occasional specimens here attain almost the dimensions of San Nicolas kelps. Holdfasts are from 1 to 4 feet in diameter, averaging less than 2, tidewater plants having holdfasts seldom 1 foot in diameter, with the exception of shore Macrocystis. Basal sporophyls are 1 to 2 feet long by 1 to 2 inches wide. Large clumps at their best have from 15 to 20 mature fronds.

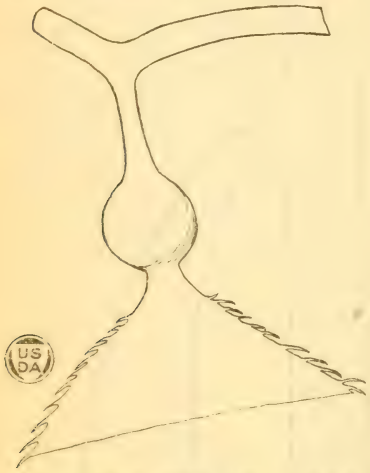

FIG. 8.—Quiet-water type—globular cyst, widely divergent.

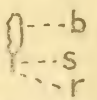

FIG. 9.—Young plant probably 3 months old. B = blade; S = stem or stipe; R = holdfast. Life size.

LIFE CYCLE OF AN INDIVIDUAL FROND.

Properly to understand all the normal and abnormal phenomena of destruction and regeneration in Macrocystis, and particularly the effects of cutting, it is necessary to consider in detail the life cycle of an individual frond. (Figs. 3, 4, 5, 9, and 10.) The clustered fruiting leaves or sporophyls at the base of the plant have been described.

If one of these leaves is more carefully examined it will be found to taper at the base to a short, cylindrical stem or stipe, the tapering base appearing to consist of much younger and more tender tissue than the stipe below or the remainder of the blade above. The teeth along its margin are also smaller and much more closely set. This part of the leaf is the region of most active growth, and might be called the "bud" of the plant. The tip of the leaf is constantly dying back and wearing away. If the leaf is fairly large a median cleft or split runs through the growing region and down into the stipe. This cleft is formed by the following process: The middle layer of the leaf dissolves into mucilage, and the outer layers sink in to form a groove on each face of the leaf; the layers of cells under the epidermis then grow very rapidly, filling up the central cavity and stretching the epidermis until the whipping action of the water splits the leaf; the rapidly growing tissue then closes the wounds and forms a new epidermis over the scars. (Wells, *10*.) Rapidly growing tissue like this is very susceptible to the action of any destructive agency, chemical or physical. After the initial cleft has been formed and the wounds have healed, the two separate parts of the leaf base continue to grow, and finally become separate leaves, the tip being torn by weathering. The divided upper portion of the stipe also lengthens a little, so that each new leaf has its own stipe. Each new leaf may repeat the process until a cluster of closely similar, short-stemmed leaves is formed. This is the only way by which Macrocystis produces basal leaves or fronds.

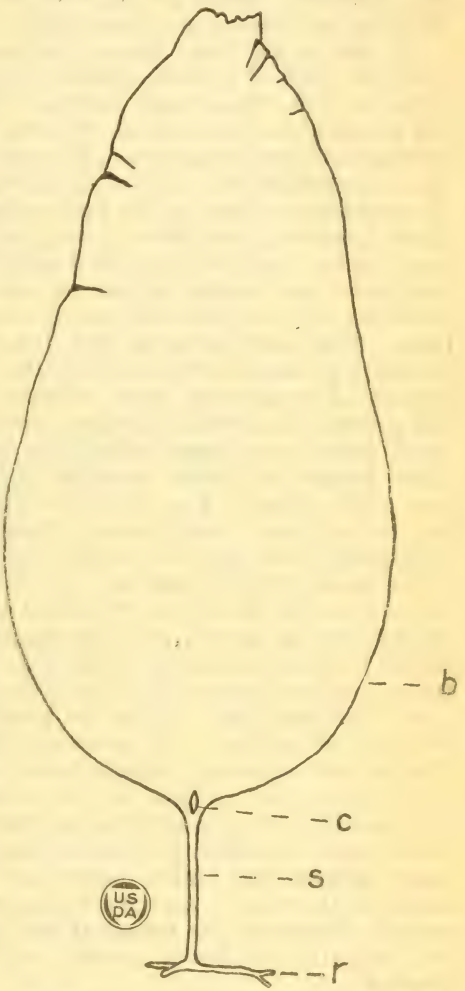

FIG. 10.—Young plant with the first split developing at C. Life size.

The manner in which a frond arises is somewhat different from that in which new basal leaves are formed. The leaf to undergo metamorphosis becomes broader than the other basal leaves and one margin grows thick and cordlike. The thickened margin ceases to produce teeth. The cleft appears in this case and runs diagonally

down to the thickened margin just above the stipe, but not into the stipe. By the time the first cleft is formed grooves for second and third have appeared in the now greatly broadened upper portion of the dividing leaf. The narrower portion of the leaf shows no indication of an additional cleft, but begins to lengthen rapidly to a narrow blade. The margin at the lower end of the cleft lengthens and thickens rapidly as the new leaf lengthens, so that the broad dividing leaf soon has a long stipe.

At this stage, then, there is a succession of leaves, splitting off from the side of a short, broad, thin leaf. These leaves differ but little, at first, from basal leaves. Their tips soon tear away from the terminal leaf coincident with the rapid lengthening of the stipe developed from its margin. The smaller leaves assume a lateral position in relation to the broad dividing leaf, but there is nearly always a conspicuous offset in the main stipe where a lateral is given off. These laterals do not develop long stipes. As they attain the size of basal leaves, the first laterals divide in the manner described above, and build up clusters of narrow, short-stemmed leaves. The stipe of about the third lateral rounds out and becomes a hollow cyst or float. The blade borne on this first cyst usually subdivides to form a cluster of leaves, which fruit later but do not send up additional fronds. Fronds may arise, however, from any leaf cluster below. All subsequent laterals develop cysts. From the fifth or sixth, upward, laterals no longer subdivide, unless accidentally split, but develop longer and much broader blades than those of leaves at the base of the plant. The first cysts formed are more plump and thinner walled than those usually found on the surface of the water. This gives them great buoyancy and enables them to hold the young frond in an upright position. As the frond grows, the terminal leaf, or, as it might be called, "terminal bud," gathers momentum in the production of laterals, until as many as 20 may be found still attached to it by their tips. (See Fig. 5.) Just as in other plants, the faster the frond grows the more delicate and susceptible to injury the "bud" becomes; but unlike the growing bud of a land plant, this bud is fully exposed. A measure of protection is afforded, however. The rapidly growing terminal leaf outdistances the laterals, especially their cysts, so that the leaves on the last two to four feet of a vigorous frond have no cysts sufficiently developed to function. Since their tissues are slightly heavier than water, such growing tips may droop several feet under the surface; thus escaping the destructive action of the wind. As the frond approaches the surface, the rate of growth decreases, the terminal leaf gradually becomes smaller and less delicate, and fewer laterals split off, until finally no more are formed.

Usually about six weeks elapse from the time a frond attains the surface until leaf formation ceases, but very thrifty fronds may grow for a longer period. After division ceases, the laterals continue to grow in length and breadth, but most especially in thickness, and the stipes continue to increase in length and weight; thus the frond is gaining weight for about three months. The growing region of the leaf gets thicker and tougher with age, so that a mature frond is able to withstand all ordinary weathering. The leaves borne after attaining the surface of the water are always smaller than those a few feet under water and the terminal leaf seldom attains the

size of the laterals. When the water is too warm for vigorous growth, some leaves next the tip do not develop. Throughout the life-cycle of the frond, all leaves, including the terminal one, weather away at the tip. In an old leaf, renewal at the base decreases and finally ceases, but the tip continues to wear away until the blade is reduced to a mere stub on the top of the cyst. Even this cyst may rot off. At the same time, animals perforate and variously abrade the leaves, thereby hastening their destruction. From a combination of causes old fronds may lose the most of their leaves. With age the cysts gradually become heavier because of the water oozing through their walls, and finally they sink. The added weight of small animals and plants which completely cover the leaves at times seem to hasten the sinking. Some small encrusting animals (Membranipora) form a bony crust on the surface of the leaves which makes them unusually brittle, and causes large numbers of them to break off and drift away. Weakening of the tissues with age or disease also results in the sloughing of fronds.

While the main frond has been growing to the surface, attaining maturity and decaying, the dividing laterals near the base have become clusters of typical sporophyls, which may continue to liberate spores, even after the upper portion of the frond has rotted away. Sometimes the upper laterals when old also develop sori. They do not subdivide, however, nor do they continue to grow after the fruiting tissue makes its appearance. Such fronds show great deterioration at the time of spore liberation. The leaves are worn down to half their normal length, the cysts are full of water, and the stipes are sometimes so weak as to break when one tries to lift the frond. Most of the color is gone, the chestnut-brown sori standing out very conspicuously from the straw-colored remainder of the frond.

The life-cycle of a frond, as given above, probably consumes from four to seven months, of which time a month or six weeks is required to attain the surface of the water. As the old frond deteriorates, a fresh one comes up to replace it.

SUMMARY OF LIFE HISTORY.

Spores are produced at all times of the year, but plants make their best growth from autumn or early-winter spores.

Spores are sticky and cling firmly to the first object with which they come in contact.

The first stages in the development of the young plant are very difficult to understand.

Young plants are not large enough to be readily discerned without a microscope until they are nearly 3 months old.

At the age of 6 months young plants are 18 inches tall or taller, and are sending up their first two fronds from two growing points.

At 9 or 10 months a plant is beginning to yield kelp in commercial quantities, and is also beginning to fruit.

After sending up the first two fronds, young plants differentiate into three types. The first does not appear to produce more than two growing points from which fronds arise; the second branches repeatedly to form a dense bush from which 20 or more fronds may

grow at a time; and the third has creeping stems which may cover extensive areas and produce innumerable fronds.

Plants often live 5 years or longer, and the creeping type may live an unlimited number of years.

Plants attain a length of from 100 to 150 feet.

GROWTH WITH REFERENCE TO ENVIRONMENT.

The important factors influencing the growth of *Macrocystis pyrifera* are substratum, depth of water, temperature, winds, waves, light, salinity, and rainfall.

SUBSTRATUM.

"The Laminariaceæ, like other fixed algæ, require a firm foothold" (Setchell, 7). Because of the great size and number of fronds spread out on the surface of the water, Macrocystis must be very firmly anchored or the winds and waves will bring it ashore. Many of the plants brought ashore are healthy growing plants which quite apparently have been torn loose from their anchorage, and it may safely be said that the kelp beds depend for their existence upon the presence of ledges or reefs, or bowlders of sufficient weight or of sufficient depth in the mud to hold the plants in place during stormy weather.

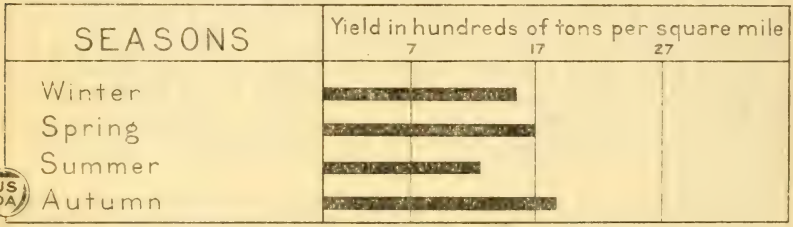

FIG. 11.—Seasonal variation in yields of kelp, 1916, 1917, and 1918. The small figures refer to yields of wet kelp in hundreds of tons per square mile of area harvested.

Soft crumbling rocks can not hold them. A great movement of sand may cover the rocks, to which kelp plants have been attached, so deep that new plants can not get a foothold there; and, on the other hand, by a similar movement of sand, rocks may be uncovered and, with other conditions favorable, kelp plants may take possession of them.

DEPTH.

Setchell has discussed the influence of depth on the growth of Macrocystis to which discussion may be added the statement that the plant makes its best growth in 40 or 50 feet of water, the heaviest mats and the longest fronds being always found overlying water of this depth. Plants growing in water deeper than this usually have much the same appearance as land plants grown in excessive shade. They apparently find it difficult to reach the surface, even when the water is still, and when there is a strong current they are often drawn far under and can not get the benefit of light. On the other hand, plants growing in shallow water lack vigor. Often their fronds are too short for profitable harvesting.

Because of the large size attained by *Macrocystis pyrifera* and the difficulty of meeting the environmental requirements, it has not been found possible to grow it in aquaria.

TEMPERATURE.

One of the most influential factors in distribution seems to be the temperature of the water. Kelps grow best in cool or cold water and are not found at all in tropical seas. Setchell states that no kelps grow on the western coast of North America in water having a temperature of more than 25° C. The waters along the mainland from Santa Barbara to San Diego have an annual range from 12° to 23° C. (McEwen, 4); the outlying islands, especially San Nicolas, are surrounded by somewhat cooler water. This variation in temperature is not too great for Macrocystis, which, according to Setchell (7), has a total temperature range of 10° to 25° C. The rate of growth is influenced negatively by the temperature of the water. (Cf. Tables 1 and 2 on yields and temperatures, respectively, and

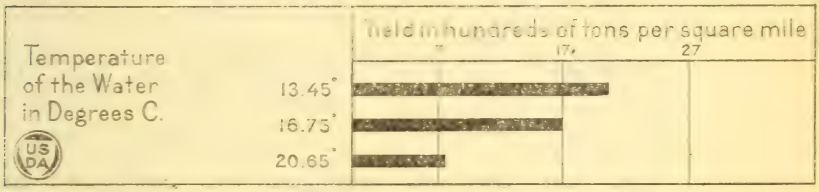

FIG. 12.—Influence of temperature on yields of kelp. 1916, 1917, and 1918. The small figures refer to yields of wet kelp in hundreds of tons per square mile of area harvested.

diagrams, fig. 11, showing seasonal variation in yields, and fig. 12, showing variation in yield with temperature, for the years 1916, 1917, and 1918.)

TABLE 1.—*Comparative harvests of kelp for the years 1916 to 1920, inclusive.*

No. of bed.	January.					February.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
1			1,846					3,900		
2								1,496		
3		25,190	14,790				26,335	8,875		
4		4,960	14,726				1,753	5,746		
5			1,110							
6			1,195							
11	1,424	5,553				3,210	3,869	2,131		
13			5,095				509			
14		1,397					1,267			
19				75					40	106
20			3,846						200	162
21				265	1,457				328	726
22					679					
23			465	190				640	95	676
24				180				1,641	50	
25										100
28				280					50	
29			45						190	
34				160						
Total	1,424	37,100	43,118	1,150	2,136	3,310	33,733	24,429	953	1,770

TABLE 1.—*Comparative harvests of kelp for the years 1916 to 1920, etc.*—Contd.

No. of bed.	March.					April.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
2			766					2,038		
3		19,540					2,500	8,740		
4		2,265								
5			4,592							
6			7,047							
7			4,592							
8			4,592							
9			4,592							
11	3,310	3,869	24			3,310	4,378			
13		3,812					2,232	6,367		
14			4,616				284			
15							138			
16		509					3,612			
19				170						
20				160	180				536	
21			985	1,088	1,311			1,141	1,457	1,120
22					479			3,163		388
23				581					108	
26			1,435							
36							3,070			
40							1,860			
43							6,175	21,560		
44			8,675							
Total	3,310	29,995	41,916	1,999	1,970	3,310	24,249	43,009	2,101	1,508

No. of bed.	May					June.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
1		900	1,950				1,465	625		
2			3,164					3,547		
3		17,726	11,998				6,950	1,175		
4		8,200	8,250				1,405			
5		1,300	3,950							
6							2,410	3,600		
7							5,850	4,379		
8							3,400	3,600		
9							3,823	3,600		
10							1,350			
11	3,310	6,001	12,591			3,310	5,997			
12		100					1,297			
13		528					4,261			
14		4,737					1,251	7,309		
16		1,019					1,022	401		
18			150					40		
20			773					80	280	892
21					916			53		780
22			496	235	1,516					
23				1,388				85	597	464
24			2,065							
25			451	128						
26								1,728		
36		1,200					1,150			
40								3,100		
41								1,700		
Total	3,310	41,711	45,838	1,771	2,432	3,310	41,631	35,022	877	2,136

No. of bed.	July.					August.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
1			1,010							
2			3,692					4,901		
3		1,200	1,200			20,000	1,200	16,525		
4						15,000				
5		450								
8		100								

TABLE 1.—*Comparative harvests of kelp for the years 1916 to 1920, etc.*—Contd.

No. of bed.	July.					August.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
10			100							
11	3,310					2,784		2,354		
12		1,508					2,092			
13		1,026	6,394				208			
14		1,106					1,368	1,780		
15								949		
16		2,151	1,112				299			
19					140					
20		202	1,104	979	1,033		216	152	162	580
21		31	310	144	209				365	
22					330				288	135
23			617					174	215	
24				161	288		206	106	105	250
25				96				97		
26			76		290				227	840
27			159					61	10	150
28		148	2,385				543	539	193	
29			787					708		
30			138				120	1,681		
31								2,035		
35							72			
37							1,984	345		
38			600				42	175		
39							87			
40		681					800			
41		7,850	22,400				14,325	2,750		
42										
43		8,450					2,050	15,175		
Total	3,310	24,903	42,084	1,380	2,290	37,784	25,612	50,507	1,565	1,955

No. of bed.	September.					October.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
1			5,043				1,400	1,105		
2			2,720					3,215		
3		4,465	465				6,975			
4		500	13,000							
5			2,335			1,075	16,135	75		
6							300			
7			135			4,680				
8						800				
10			600				600	248		
11	4,165		57			4,165		1,960		
13							6,912			
14		4,563	47					900		
15			20							
16		680	200				117			
17			97							
18								419		
19				75					60	110
20			80	87	972			434	260	695
21				350					668	
22				75				314		150
23								65		
24									160	
25									643	
26					645			231		
27					128					995
28			25		620			710		
29			90					135		
30		1,106	529				2,218	116		
31			3,760					11,849		
32			441					129		
33			651					350		
37			510					550		
38			440							
40		435					142			
41		6,490	4,150				350	4,725		
42							373	700		
43	14,970	14,500						5,550		
Total	19,135	32,739	35,395	587	2,365	10,720	35,522	33,780	1,791	1,950

TABLE 1.—*Comparative harvests of kelp for the years 1916 to 1920, etc.*—Contd.

No. of bed.	November.					December.				
	1916	1917	1918	1919	1920	1916	1917	1918	1919	1920
	Tons.	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*	*Tons.*
1		285								
3	8,055	1,000				22,795	4,000			
4	4,640									
5							4,350			
6		1,920								
7		1,920								
8		1,920								
9		1,920								
10		3,120								
11	5,062					5,062				
12		5,531								
14							7,913			
15							235			
16		1,871					1,291			
19							1,600			
20		611		448	805		64			1,556
21				250					1,315	
22					565					728
24		439		215	128					
25				271	130					
26		529			440		106			
27					600					
28		840					1,101			
30		376								
37							3,175			
40		800					122			
41		10,025								
42							20			
43		3,475					7,220			
Total	17,757	36,582		1,184	2,668	27,857	31,197		1,315	2,284

Year 1916..... 134,537 Year 1918..... 390,863 Year 1920..... 25,374
Year 1917..... 394,974 Year 1919..... 16,613

TABLE 2.—*Monthly averages of the surface temperatures of the ocean as recorded at the Scripps Institution for Biological Research, at San Diego, from January, 1917, to March, 1919, inclusive.*

Month.	1917	1918	1919	Normal.[1]	Month.	1917	1918	1919	Normal.[1]
	°C.	°C.	°C.	°C.		°C.	°C.	°C.	°C.
January	12.72	14.02	14.36	15	August	22.03	21.54		18
February	12.27	13.55	14.26	15.6	September	20.12	20.35		18
March	13.94	14.62	13.85	15.6	October	18.34	19.76		17.5
April	15.16	15.56		15.6	November	16.49	17.02		17
May	16.65	17.88		15	December	16.36	14.82		16
June	19.26	20.46		17					
July	22.05	21.18		17	Mean	17.12	17.56		16.44

[1] According to Thorade (*9*).

WINDS.

All the heavier, more vigorous kelp beds along the mainland and island coasts of southern California lie fully exposed to the wind. One may safely say that the more exposed the kelp is to the wind, the more vigorous are the plants. The strong winds and rough seas of San Nicholas and other outlying islands have given rise to kelp with heavy stipes and thick, tough, leathery leaves of a deep chestnut brown color. On the other hand, the kelp growing in the quiet waters of the island coves has slender stipes and broad, thin leaves

of a pale yellowish brown color, and very brittle texture. The extensive kelp beds of the Santa Barbara coast, which are more sheltered from the wind than are most of those farther south, are characterized for the most part by rather light kelp. These latter beds seem also to deteriorate more in warm summer weather than do any others along the coast.

Light winds keep the air circulating, thereby preventing overheating of the stratum immediately overlying the water. These winds splash water over the floating portions of the kelp which are thus

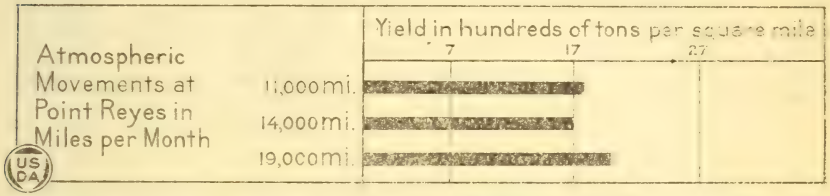

FIG. 13.—Variation in yields of kelp with moderate winds, 1916, 1917, and 1918. The small figures refer to yields of wet kelp in hundreds of tons per square mile of area harvested.

kept cool by evaporation. The prevailing northwest wind of the central Pacific coast is regarded as one of the chief causes of the upwelling and southward drift of cold water along the coast (McEwen, 4). The southern limit of this upwelling and the southern limit of Macrocystis are said to coincide very nearly. On account of their being the best available index of the prevailing winds of the greater part of the California coast, the Point Reyes wind records are included in the tables. (See Table 3 and fig. 13). It is very probable

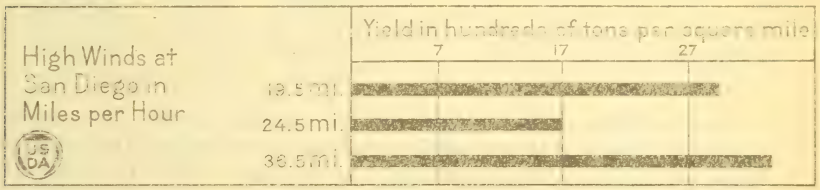

FIG. 14.—Variation in yields of kelp with high winds, 1916, 1917, and 1918. The small figures refer to yields of wet kelp in hundreds of tons per square mile of area harvested.

that the much lighter winds recorded at San Diego also have considerable influence on the movement of the adjacent water. (See Table 4 and figs. 13 and 14.) Often when the wind is blowing from the southwest or west, kelp of the type peculiar to the islands is brought into the beach at La Jolla in an excellent state of preservation. Such winds may also influence the temperature of the water.

TABLE 3.—*Total monthly atmospheric movements and prevailing direction as recorded at Point Reyes Light.*

[Miles per month.]

Month.	1917	1918	1892–1918 average.
January	12,864 NW.	14,134 NW.	13,543 NW.
February	14,821 N.	15,368 NW.	12,878 NW.
March	20,638 NW.	11,333 NW.	15,580 NW.
April	14,454 NW.	18,617 NW.	16,702 NW.
May	21,369 NW.	23,237 NW.	19,194 NW.
June	22,719 NW.	16,133 NW.	19,602 NW.
July	14,944 NW.	16,861 NW.	16,522 NW.
August	11,586 NW.	13,140 NW.	14,545 NW.
September	12,443 NW.	9,813 NW.	12,972 NW.
October	9,509 NW.	12,923 NW.	12,698 NW.
November	9,861 NW.	11,616 NW.	11,776 NW.
December	11,052 N.	12,831 NW.	12,133 NW.
Mean	14,688 NW.	14,667 NW.	14,845 NW.

TABLE 4.—*Total monthly atmospheric movements and prevailing direction as recorded at San Diego.*

[Miles per month.]

Month.	1917	1918	1892–1918 average.
January	3,853 E.	3,982 E.	3,928 variable.
February	3,972 NW.	4,579 W.	3,903 NW.
March	4,645 NW.	4,464 NW.	4,582 NW.
April	5,299 W.	4,589 W.	4,546 NW.
May	5,659 SW.	5,325 SW.	4,763 W. or SW.
June	4,295 W.	4,697 W.	4,376 W. or SW.
July	4,342 W.	4,864 NW.	4,354 NW.
August	4,661 NW.	4,901 NW.	4,261 NW.
September	4,273 NW.	4,524 NW.	4,130 NW.
October	3,749 NW.	4,172 NW.	3,920 NW.
November	3,329 NW.	4,186 NW.	3,703 NW.
December	3,075 NW.	3,838 E.	3,746 NW.
Monthly mean	4,263 NW.	4,510 NW.	4,184 NW.

As noted before, even a light breeze causes ripples that splash over the kelp, keeping it wet and cool, but these ripples are soon lost in a thick bed of kelp, and perhaps it is because of this fact that the largest and most virgorous plants always occur near the edges of the bed, while dead and decaying material appears first in the heavy mats.

Strong winds are continually recharging the water with air. Setchell (7) states that kelps require a great amount of air: that some forms, such as Postelsia, grow only in the surf on the most exposed points, where they are continually bathed in spray. One of the first things discovered in growing kelps in aquaria is the necessity of working an abundant supply of air into the water. The air worked into the ocean water by the action of the wind, seen in the formation of "whitecaps," is mainly brought to the plants by surface drift. In very windy weather, however, the kelp fronds are whipped about and oftentimes fragments and even whole plants are torn away.

WAVE ACTION.

Waves themselves are necessary to keep kelps alive and growing. Macrocystis does not usually grow in the surf. It seems to require deeper water in order to make its best growth, as its leaves are too fragile to withstand the wrenching and pounding of the breakers. San Pedro breakwater furnishes an excellent place in which to study the effects of waves on the distribution of kelp. The very tough ribbon kelp (*Egregia laevigata*) completely fringes the weather side of the breakwater, where it receives the full impact of the breakers. No Macrocystis grows here, but just beyond the breaker line it is abundant. On the lee side of the breakwater, on the other hand, there is a rich variety of seaweeds, in which Macrocystis is prominent. Here streams of water rush through the crevices after a big wave strikes the weather side. During the winter and early spring, with the aid of the great quantity of driftwood that accumulates, the waves wear away the plants in the tidewater zone faster than they can grow up, and for considerable areas the rocks are completely stripped. In the calm weather of spring, growth begins in crevices, pockets in the rocks, and other less exposed places. Egregia is the first to appear and Macrocystis comes a little later. When growing under some protection Macrocystis makes a more vigorous plant, with a longer primary stem or stipe, than when growing in an exposed place. Where the water falls in a small cascade on the bare face of a rock, kelp plants do not appear until small plants and animals have covered the surface.

STORMS.

Kelp beds are sometimes seriously depleted or even completely torn out by storms. For example, the Point Loma kelp bed was completely torn out by the great storm of the winter of 1888–89 (Davidson, 7), and the same kelp bed, as well as the La Jolla bed, was reduced nearly 40 per cent in area, besides being greatly thinned by storms in the late winter and early spring of 1915. Strong northwest winds are usually not very destructive, because they have little effect on the size of the waves, and because they are very frequently accompanied by a strong current that holds most of the kelp down out of harm's way. Southwest winds, on the other hand, usually raise a violent swell and usually there is not enough current to keep the plants submerged. Under such circumstances, a plant near the outer edge of a kelp bed may become detached from its anchorage or, if attached to a rather small stone, may "drag its anchor." No matter in what way a plant begins to drift, it always floats with its holdfast under water. Drifting through the bed, the fronds of the first plant with which it comes in contact enwrap the holdfast. Presently the second plant with its double burden of fronds lets go, and the mass starts through the bed, increasing in volume and destructive power as it travels. Thirty or more plants sometimes come ashore in one single "drive." The thicker the kelp beds the greater the destruction is likely to be in the more violent storms.

SALINITY AND RAINFALL.

Rains probably affect the growth of the plant but little. Coasts inhabited by it vary in rainfall from 10 to 60 or more inches per year. (See McFarland (*5*), and Bartholomew (*1*).) The author has seen fairly healthy plants of Nereocystis growing in the brackish estuary of Big River at Mendocino City; and it is a well-known fact that numbers of sea-weeds grow on the steamboats plying between Stockton and San Francisco, in spite of their being subjected to daily changes from fresh river water to salt sea water and vice versa. (Osterhout (*6*), pp. 227–230.)

LIGHT.

The kelp plant contains chlorophyl and manufactures starch from CO_2. It must, therefore, like green land plants, have light. No kelp is found in the dense shade under the oil docks on San Pedro breakwater, although there is an abundant growth at both sides of them and between them. It also seems to make a poor growth where it is shaded by a high bluff. On the other hand, just as in the case of land plants, very strong light appears to retard its growth. Plants near shore almost invariably have shorter and fewer fronds than plants growing in deeper water; and the fronds of shallow-water plants seldom float on the surface for more than 15 feet, whereas 50 feet is not an unusual length for the floating portions of plants growing in water of a depth of 40 to 60 feet. Light may also have much to do with the reduction of rate of growth, and finally the complete cessation of growth in a frond after it has attained the surface of the water.

SEASONAL VARIATION IN CONDITION OF KELP BEDS.

In summarizing the subject of growth, owing to the influence of the various factors enumerated above, Macrocystis is restricted in its distribution to more or less widely separated groves along the sea coast, plants within the groves vary greatly in size and vigor, and the groves themselves vary greatly from year to year in density and in area. There is, moreover, a comparatively regular seasonal variation in the amount of kelp floating on the surface. July and August may be called the dormant season, since few new fronds are coming up at that time and the old ones are rapidly decaying and disappearing. In September, or early October, activity is resumed and if the water is cool, and storms are not too frequent, December sees a heavy mat of kelp on the surface. The frequent windstorms of January, February, and March cause rapid wearing away of the leaves and destroy many fronds and even entire plants, so that although the plants are growing with maximum rapidity at that season, the quantity of floating kelp is somewhat reduced. In April, with the continued rapid growth of the plants and the less frequent occurrence of storms, the density of the floating mat is soon restored, and this heavy mat persists until June, when, with the warmth of the water increasing, decay begins to gain on regeneration. In the tables, the yield of kelp per unit of area is taken as an index of the rate of growth. Such a conclusion may seem unfair, since the entire area of

a grove is given in the tables, although that grove may not have been entirely cut over in any given month; but, on the other hand, the areas of certain other groves are omitted as not having been cut over at all, it being the custom of most harvesters to cut the same portions of a kelp bed two or more times in a month and leave other beds uncut, either because they are not considered worth cutting or because of unfavorable weather or distance.

The great reduction in yield per unit area in the summer months is due in part to the cutting of thin groves which have been passed by in the winter, when kelp was plentiful and cutting difficult and dangerous.

Sporulation or fruiting of Macrocystis, like growth, is practically continuous throughout the year, but varies in amount with the seasons. Unlike the floating fronds, the fruiting leaves escape the destructive effects of storms, as they are borne near the base of the plant.

In the dormant season the fruiting areas are reduced to small patches on a few of the fertile leaves, or sporophyls, at the base of the plant, but in the middle of the growing season practically the whole area of every sporophyl is pressed into service. Vertical hauls from bottom to surface made at the edges of a kelp bed, with a towing net of No. 25 bolting silk, revealed the greatest number of free swimming spores in the autumn. This fact, however, does not indicate that there is less spore production in winter than in autumn, since the spores produced in winter appear to settle much more quickly.

As to the fruit itself, the spore-producing areas are not restricted to grooves. Their appearing to be so is due to their being worn away from the ridges of corrugated sporophyls. The thousands of fruiting leaves that have been examined have shown both perfectly plane and deeply corrugated surfaces.

In the summer the sori are restricted to small, irregularly rounded blotches, but in winter they completely cover the sporophyls developing from the base as the sporophyls at the tip liberate their spores and disintegrate. The sori occur as thickened, opaque areas, richly colored and soft in texture.

DESTRUCTION BY NATURAL AGENCIES.

In addition to the normal thinning of kelp beds in summer by deterioration, disappearance of old material, and decreased growth, entire kelp beds sometimes disappear. Sometimes this extensive disappearance is due to decay unaccompanied by regeneration. In the vicinity of Santa Barbara, heavily matted kelp beds have been known to sink and not reappear for months. Several beds disappeared in that way in July, 1917. Many persons claim that kelp beds in that vicinity have disappeared similarly in the past, but since the reports do not agree as to time, they can not be used as data. The 1917 sinkings were not studied closely enough to yield any but theoretical explanations. The immediate cause of such sinking could readily be overlooked because a current not visible from shore might completely submerge a kelp bed for several days at a time.

Of the various explanations offered for the phenomenon, only two need be mentioned here. The first is that the heavy mat of kelp, composing the affected beds, shut off the light from the leaves below; that this rendered them unable to manufacture the usual amount of starch, and evolve sufficient gas to keep the cysts full; that the cysts then filled with water, the fronds below sank and dragged down the floating mat, which thereupon decayed. There are two important objections to this theory: First, the solid tissues of kelp are but slightly heavier than water; therefore, even though the cysts on the under side of the mat should become completely filled with water, the water-logged portions would exert only a slight downward pull. So long as the upper layers of the mat remained healthy, they would retain their buoyancy, and the bed would not sink. Second, kelp decays much less rapidly under water than on the surface. Plants that never rise to the surface, except when there is no current, are vigorous and free from disease. If a heavy kelp bed which has just begun to slough should be submerged for a few days by a strong current, it would probably be clean and healthy when it rose again to the surface.

The more plausible explanation is that the kelp died and decayed during the hot wave. The United States Weather Bureau reports unusually warm weather in the Pacific coast section in July, 1917. Capt. W. Engelke reports that a heavy bed of kelp off Canada del Capitan completely disappeared in four days' time during a hot wave early in July. At the same time, another bed a few miles to the east also disappeared, but a third bed lying between the two survived. This middle bed lay opposite the mouth of a canyon where, unlike the other two beds, it was exposed to a slight land breeze during the hot wave. The water over the area where the kelp had disappeared showed the color imparted by decaying kelp. The objection may be offered that kelp does not decay so rapidly; but in warm weather kelp plants are often thrown up, fresh, in the morning, on the beach at La Jolla, and by midafternoon their sporophyls are rapidly decaying. Young plants carried in an iron collecting box, in fairly warm weather, decay to such an extent in 24 hours that they fall apart when lifted from the box. In explanation of the kelp's sinking, instead of sloughing and drifting ashore, Mr. Thompson, at Summerland, suggested that the cysts developed punctures and then filled with water and sank. Numerous observations in the laboratory and in the kelp beds prove that when kelp lies exposed to the air for several days, in perfectly calm weather, the upper exposed side of the cyst soon decays and develops a puncture. In comparatively open kelp beds, when there is plenty of wave motion and the cysts have no chance to become dry or sunburned, no puncturing occurs. But the Santa Barbara kelp that sank was all densely matted and in three or four days of perfectly still, warm weather, enough puncturing could have occurred to sink it.

These kelp beds were slow to reappear, the one at Canada del Capitan not appearing again until the following March. From various observations of dead holdfasts, and from data recently gathered on the development of young plants, it seems safe to say that the old plants in these beds all died, and that the new beds of 1918 were made up entirely of young plants derived from spores

which had been disseminated very soon after the old plants died. From October to December, 1917, enormous numbers of dead holdfasts, with their stipes completely gone, were found on the beaches at Santa Barbara. These holdfasts were black, whereas the holdfasts of a plant washed up by the waves normally is brown when it comes ashore, and it changes color but slightly in drying. Moreover, black holdfasts, not differing in the least from those on shore, were seen coming in in the surf. Such holdfasts were found along the coast as far south as La Jolla, but nowhere in such numbers as at Santa Barbara.

In addition to the two just described other kelp beds near Santa Barbara practically disappeared. Puncturing and sinking may have occurred in these beds, but probably much of the destructive work was done by the bacterial disease, black rot, which destroys the kelp piecemeal, but very effectually, nevertheless. This disease, to be described presently, may have been responsible for the many dead holdfasts.

None of the more exposed kelp beds farther south, or around the islands, sank, although those along the mainland became thin. During the same warm weather the temperature of the water at La Jolla rose at one time to nearly 24° C., within 1° of the upper limit for kelp. It is therefore not unlikely that at some points along the sheltered Santa Barbara coast the surface water at least may have risen above the 25° C. limit of temperature.

The water cooled noticeably in September (Table 2), and the kelp beds soon began to recover. Growth became more and more vigorous as the water cooled and winter weather came. By spring the kelp beds were yielding heavily (see Table 6 and fig. 11), and the supply was adequate. By midsummer the kelp was deteriorating, and by October there was a serious shortage, only half as much, approximately, some beds having practically disappeared. This time, however, the cause of the disappearance was plain.

TABLE 5.—*Highest wind velocities attained at San Diego in successive months in 1917 and 1918, with direction at the time of highest velocity, in miles per hour, taken as an index of stormy weather.*

Month.	1917	1918	1892–1918 average.	Month.	1917	1918	1892–1918 average.
January	33 S.	33 S.	28	July	21 NW.	20 NW.	20
February	34 S.	34 S.	30.4	August	17 W.	20 S.	19.6
March	24 NW.	24 NW.	30.3	September	27 NW.	22 S.	21.2
April	43 S.	43 S.	25	October	26 NW.	22 S.	21.1
May	24 S.	24 S.	25.1	November	25 S.	32 NW.	24.3
June	20 NW.	30 S.	20.1	December	17 NW.	35 W.	26

The winds had been practically the same as in 1917. (See Tables 3 and 4.) The water, in July and August, had risen to almost as high a temperature as in 1917 and had remained so high that in October it was warmer than in the same month of the preceding year. In addition to lack of air and water circulation, and to the high temperatures, the weather was unusually cloudy. Early storms in September and October (Table 5) also, did great damage to some of the beds.

TABLE 6.—*Approximate areas of kelp fields in which harvesting was carried on in the various months of 1916, 1917, 1918; with the average quantities of kelp cut per square nautical mile.*[1]

[Tons of wet kelp.]

Month.	1916		1917		1918	
	Square nautical miles.	Tons per square mile.	Square nautical miles.	Tons per square mile.	Square nautical miles.	Tons per square mile.
January	1.26	1,130	9.09	4,124	11.82	3,649
February	1.26	2,603	9.26	3,603	12	2,221
March	1.26	2,603	8.53	3,514	11.83	3,543
April	1.26	2,603	12.90	1,810	9.96	4,319
May	1.26	2,603	12.10	3,447	15.36	2,851
June	1.26	2,603	16.17	2,575	29.34	1,194
July	1.26	2,603	21.38	1,165	28.25	1,489
August	7.36	5,125	35.06	730	36.55	1,382
September	3.26	5,823	24.94	1,313	47.04	753
October	3.03	3,617	25.02	1,420	37.29	906
November	7.36	2,409	33.93	1,078	.....	.....
December	5.06	5,608	18.42	1,693	.....	.....
Mean	2.9	3,277	18.9	2,206	[1] 23.94	[1] 2,230

[1] Computed on the basis of 10 months' records.

BLACK ROT.

Black rot was observable in some places as early as April. It gradually increased where the kelp was not cut, until by August it was in complete possession in most of such beds. In uncut beds, the summer growth was scant and light in weight. Beds which had been cut closely and systematically as late as May or June, were free from disease, and had the normal number of young fronds. These fronds, however, did not mature properly. Their stipes remained slender and their leaves pale, small, very thin, and of the texture of paper. The plump, thin-walled cysts characteristic of kelp growing in quiet water appeared in places. The weakening effect of unfavorable growing conditions was noticeable in the tips. They dwindled down, failed, usually, to develop the last leaf-blades, and, in some cases, ceased to grow while they were still throwing off laterals. The chemical composition was also affected. Kelp manufacturers in general complained that the material was watery and yielded only half the normal amount of potash, and the Hercules Powder Co., stated that it did not properly ferment.

The United States reserve bed at Summerland may be taken as an example of extreme deterioration, since it was barely visible from shore. It had never been cut over clean, and, as a result, had become, in early summer, a veritable breeding bed for black rot. Many old spring fronds could be seen floating lightly, their leaves entirely gone and nothing but stipes and some cysts left. These were of good length, ranging from 30 to 40 feet. Rising beside the dismantled stipes were the midsummer fronds, some of which had reached the surface and floated out for a few feet, but many were from 1 to 4 feet under water. Their lower leaves were of normal size, but the tips were noticeably shortened. That these fronds had stopped growing was indicated by the fact that the color of the tips was the same as that of the older leaves, whereas rapidly growing tips are light olive green. Probably the warmer surface water

had checked their growth. Comparable to these stunted plants were a number of plants of elk kelp (Pelagophycus) observed on the edge of the La Jolla bed in November, 1917. These specimens were fully matured and decaying plants, yet they had never attained the surface, but stood erect, with their cysts 10 to 20 feet under water.

During the cool, stormy weather of November and December, 1918, the kelp beds improved noticeably. During the following months they gradually returned to their original density, responding to changes in water temperature and weather. Unfavorable conditions later on resulted, however, in the nearly total disappearance of kelp beds along the San Diego coast, with the exception of the bed off Point Loma where there is an unusually free circulation of water, and where the temperature of the water is low.

There is little doubt that black rot is the most destructive enemy of kelp. This disease attacks all the beds along the south California coast, including those around the islands, and destroys more kelp than storms do. It does no appreciable damage in the winter, but attacks the spring and early summer growth which would otherwise be the best to harvest. Between April and July, 1918, it ruined a fine bed of kelp at Naples; thus, where 3,000 tons could have been cut in April, only 300 were available in July when the bed was opened. The United States Government reserve bed at Summerland, as stated above, became a veritable bed of black rot. By August, wherever the harvesters had not cut, the disease had possession of practically every frond, even in the wind-swept beds of San Nicolas. The disease was reported to have destroyed much kelp in the summer of 1917, and it probably also destroyed the San Nicolas beds in the summer of 1915, and the heavy Mexican beds in the late winter and spring of 1919.

Black rot is a bacterial disease, but the species of bacteria has not yet been classified. However, sufficient information has been obtained, from experiments in the laboratory and observations in the kelp beds, to enable us to formulate a plan of control. The organism does not grow readily at a temperature as low as 15° C., and, consequently, practically disappears during winter. It thrives in a temperature of 18° to 20° C. It has been found to require a great deal of air. When infected plants were placed in a vessel of sea water and covered to exclude all air but what was dissolved in the water, the bacteria of black rot were speedily displaced by ordinary fermentation bacteria. This behavior of the organism in the laboratory is paralleled by its not working under water to any noticeable extent in the kelp beds. It apparently requires more air than is dissolved in the water.

The plants which black rot has been observed to attack are long bladder kelp (*Macrocystis pyrifera*), elk kelp (*Pelagophycus porra*), and ribbon kelp (*Egregia laevigata*). Of these, the last is seldom attacked, because it floats for the most part under water, except in the tidal zone, where the surf beats off and carries away any weakened or decayed material. Pelagophycus, while very frequently attacked, is not destroyed in such quantities as Macrocystis, probably because the more delicate parts are usually under water. The disease mainly attacks leaf blades, which present many wounds and

abrasions, especially the surface layer, through which it can enter. Fronds are not attacked until mature or nearly mature, when they have more of a tendency to float on the surface. The frayed and decaying tip of the blade affords the most common entrance. (Fig. 15.) A young lesion appears as a small, semicircular, dark-brown spot at the torn edge of the blade. This spreads very rapidly until it becomes a broad band crossing the upper end of the leaf. The affected tissue turns nearly black, becomes soft, and soon weathers off. Infection spreads rapidly to adjacent leaves, and soon after its first appearance the disease destroys the entire floating portion of the frond. In badly perforated leaves infection sometimes takes place in a dozen parts at once. Where growing tips float on the surface, as they sometimes do in heavily matted kelp, their delicate tissues are readily susceptible to attack. Sometimes growth is arrested by the young stipes becoming infected. Infections of the epidermis usually appear as circular dots. Below the blackened region the color fades from the normal brown to dingy yellow. After destroying the blade, the disease attacks the cyst and later the stipe. (Fig. 16.) These parts do not blacken usually, but turn rusty brown and later white when the decayed surface layers dissolve off from the colorless interior layers. Affected fronds generally weaken and slough off gradually. More noticeable, however, is the breaking off of the cysts, which sometimes drift in on the beaches in enormous numbers. Old dismantled stipes may remain attached until they dissolve or sink, because with the leaf blades gone there is nothing for wind or wave to catch.

FIG. 15.—Young leaves at the tip of a nearly mature frond attacked by black rot.

Why black rot does not usually cause a frond to sink becomes clear if we examine the structure of the wall of a cyst. The first layer or two of cells contain color granules, are assimilating layers, as are the corresponding layers in the expanded blade, and absorb water readily, being always filled with water in the living plant. Their outer surface is more or less slimy. The next layers are composed of colorless, closely packed, thin-walled cells, also fully charged with water, which make up a tissue resembling that of a summer turnip. The inner layer consists of felted fibers presenting a dry silky surface with loose bits of weft here and there. This inner layer keeps water out of the cyst. The other layers may be removed, but no water can enter the cyst if this inner layer is not impaired. Since black rot works inward, it can destroy the outer layers of a cyst without impairing its buoyancy. On the contrary, by destroying the leaves first it renders the fronds unusually buoyant.

The new fronds sent up from the base of a diseased plant are usually clean and healthy until they attain the surface, although plants are sometimes weakened throughout, or even killed, the delicate spore-bearing tissues perishing first. The lower submerged portions, however, are not directly attacked. Since black rot becomes

more destructive as the temperature of the water increases, it may be an important factor in limiting the distribution of kelp.

As is the case with all bacterial disease, liability of the plants to attack is conditional, to a great extent, upon exposure to the organisms and upon the number of organisms present. Since the organism is very effective only on the surface of the water, plants held under water by currents escape. Severe weathering also affords considerable protection by removing diseased portions. Thorough periodic harvesting is especially beneficial in that it removes all diseased portions. The season for preventive cutting is dependent upon a number of factors. The disease is equally effective, apparently, in heavily matted and in rather open kelp. The temperature of the water and the amount of wind and current are probably the important factors. One cutting in May or June might suffice for a well-exposed bed, whereas, in a quiet sheltered place, a bed

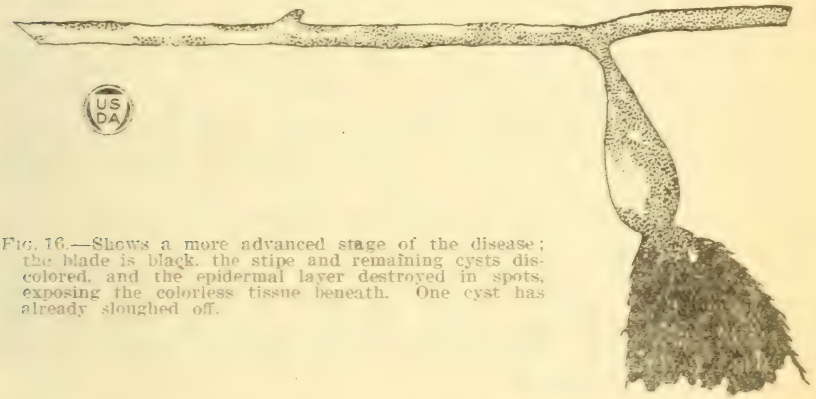

FIG. 16.—Shows a more advanced stage of the disease; the blade is black, the stipe and remaining cysts discolored, and the epidermal layer destroyed in spots, exposing the colorless tissue beneath. One cyst has already sloughed off.

would probably need to be cut first in March or April and again in June or early in July. When the disease appears in a bed that bed should be thoroughly cut over as speedily as possible.

METHODS AND EFFECTS OF HARVESTING AND YIELDS.

A number of methods of harvesting have been employed, the most primitive of which is to gather the kelp as it is washed up on the beaches. This method is the least efficient of all, because so much material is lost by sinking and by coming ashore in inaccessible places. A second method is to pull up clumps of fronds by means of a cable and hoist. This method uproots and destroys many plants. Fortunately it is more difficult and expensive than cutting and has not been employed to any great extent by commercial harvesters. The third method, the one usually employed by the so-called hand-pickers, is to drag fronds into a skiff or small barge by means of a boat hook, and cut them off with a long knife, as far down in the water as is convenient. By this method the plants are left in place to send up more fronds and all the kelp cut is saved. Too much hand work is required, however, to make it practicable on a large scale.

MOWING.

The fourth method of harvesting, used by all the large establishments, consists in mowing the kelp. For this purpose a vessel is equipped with a more or less complex machine, of which the essential parts are a horizontal cutting blade working on the same principle as a mower knife, at a depth of about 4 feet, and an endless chain elevator, or "draper," which hoists the kelp on board. Various types of vessel have been used, but in all that have been operated successfully the harvesting mechanism is placed in the bow, the blade cutting directly ahead of the boat. The length of the knife is considerably less than the beam of the boat, the largest harvesters cutting a swath some 20 feet wide and the smallest about 10. The elevator has the same width as the swath. Its lower sprocket wheels are immediately back of the cutter bar, and it is driven at rather high speed, so as to pick up the cut kelp before the waves wash it away. A knife at each side of the elevator, and parallel with it, serves as an edging knife to cut the kelp clear at the sides. There being no tough, hard fiber in kelp, the knives cut properly at about one-fourth the speed at which a mower knife must work. A gasoline motor drives the harvesting mechanism. When not in actual operation the knives are hoisted out of the water. The great bulk and weight of machinery in the bow of a kelp harvester make it difficult to steer, especially in rough weather. Such a device as described above, when properly adjusted, may cut a hundred tons of kelp without uprooting a plant. However, if the weather is rough, or if the knives are not kept running properly, it may uproot large numbers of plants. The elevator fails to pick up many of the fronds and they are washed away by the waves. Sometimes nearly half the kelp cut is thus set adrift. Various methods are used in loading the kelp after it is brought aboard.

METHODS.

Two methods of mowing have been employed: cutting systematically up and down or round and round a bed, as in cutting hay; and running the harvester through the bed so as to cut the thicker portions only. The first method was employed by the Hercules Powder Co., with good results. By employing three large capacity harvesters simultaneously, which cut one behind the other, only a small proportion of the kelp was lost, as one harvester picked up what the one before it set adrift. Rapid and thorough cutting tended to keep black rot under control and to protect the new growth that came up almost immediately after cutting from molestation. The disadvantage connected with this method is the loss of time and labor in cutting over thin portions of the bed.

COMPARISON OF METHODS.

The second method of cutting is the one that has usually been employed. It has the outstanding advantage of saving time at the start and of insuring the getting of the best kelp. When several companies are cutting in the same bed, there is often considerable competition for the best portions. An advantageous modification of this method is to avoid cutting to the edge of the bed,

so that the drift kelp may be caught by the uncut plants and picked up later, unless a strong current happens to submerge the attached plants, in which case, of course, all loose material would be carried away. The disavantages in this method are that, in the long run, time is lost because cutting swaths and patches here and there soon leaves a bed spotted, and there is then no good cutting anywhere; that when the current is strong, or the harvester careless, more kelp is lost, because it is set adrift on both sides of the swath; and that, if the heavier clumps are cut over several times—as is likely to be the case in a month's harvest—all the first new fronds are topped, and the renewal of the bed thereby delayed; furthermore, that with the thinner portions left uncut, the full yield of a bed is not obtained, and, besides these uncut portions may become breeding places for black rot.

PERIODS OF HARVESTING.

In some of the kelp beds harvesting was carried on continuously for a period of from 4 to 12 months, or even longer, whereas other beds were cut periodically, with 2 months or more allowed for regeneration after each cutting. The former method was employed where there appeared to be an ample supply of kelp near at hand, and in some cases, where harvesting operations could be carried on only in summer, as at San Nicolas Island, or where a distant bed was used to make up for shortages. Such a system of harvesting has the advantage of clearing out any diseased plants, also of keeping the bed open to sunlight and circulation, but sooner or later the plants begin to weaken as a result of such severe pruning, and periodic cutting seems to be the better method. Periodic cutting controls black rot if the kelp is thoroughly cleaned off each time, and it tends to regulate growth and thereby to make the product uniform. Three or four months seems to be the proper time to allow for growth after cutting, as a large proportion of the fronds reach maturity in that time. If longer rest periods are allowed, deterioration begins, the older fronds sloughing or becoming covered with small plant and animal forms and the liability to loss from storms or disease being increased.

In order for the supply of kelp to be continuous, the beds must be cut in rotation. Each section should be of no larger size than can be completely cut in a month, and it is still better if cutting does not continue for more than two weeks in a given section. Considerable latitude must be allowed, however, because strong currents may hold down the kelp and delay cutting, storms may interfere with the cutting of distant beds, or the occurrence of black rot may make it necessary to hasten cutting. Since kelp grows most in winter and least in summer, harvesting should be carried on as extensively in the winter as the weather permits, and practically discontinued in midsummer and early autumn. Such a system would accord well with the annual fluctuations in the California labor market.

YIELDS.

The tables compiled from the reports on yields by the California State Fish and Game Commission (1916 to 1920 inclusive) show the comparative effects of continuous and periodic harvesting. In these

tables only such beds are considered as have been regularly cut for a period of two years or longer. These beds are separated into two groups, according to whether cutting in them was continued for 4 months or more at a time, or for only a month or two. Table 7 consists of the beds in which continuous cutting was practiced. Some were cut continuously for the first 12 or 13 months, but when they began to weaken they were given a rest and cut periodically thereafter. In other cases, for example at Santa Barbara and San Nicolas Islands, more or less cutting was done every month for 4 or 5 months, and the kelp was allowed to grow, perhaps for the rest of the year.

Table 8 consists of those beds in which periodic cutting was practiced throughout the time they were harvested. From some of the largest of these beds cuts were reported in three consecutive months, but in such cases the beds were divided into sections, cutting probably not continuing more than a month in any one section.

The difference in the tons of kelp cut under the two systems for the three years (omitting November and December, 1918) are shown in Tables 7 and 8.

TABLE 7.—*Cutting continuously for five months or more at one or more times since harvesting began.*

Number of bed.	1916	1917	1918	Number of bed.	1916	1917	1918
	Tons.	*Tons.*	*Tons.*		*Tons.*	*Tons.*	*Tons.*
3	50,850	115,881	63,668	40	.....	4,840	3,100
11	39,738	29,670	19,117	41	.....	39,040	35,725
13	.....	19,448	17,855				
14	.....	23,886	14,572	Total	.....	245,336	155,750
16	.....	12,571	1,713				

TABLE 8.—*Cutting periodically, allowing two or three months for growth between harvests.*

Number of bed.	1916	1917	1918	Number of bed.	1916	1917	1918
	Tons.	*Tons.*	*Tons.*		*Tons.*	*Tons.*	*Tons.*
1	.....	4,050	13,633	8	800	5,420	8,192
4	19,640	34,718	41,722	9	.....	5,743	8,192
5	1,075	7,175	12,062	43	.....	42,340	56,785
6	.....	4,630	11,842				
7	4,680	7,770	9,106	Total	.....	111,846	161,534

The kelp beds from Point Dume to Point Conception are omitted from the comparison because no cutting was done in the section beyond Ventura until July, 1917, and operations ended in January, 1919. Other beds not mentioned in the tables were cut only at rare intervals to make up a shortage, a number of them not being opened for cutting until 1918.

OPPOSITION.

In the past some objections to cutting have been raised by the uninformed, the claims being that it kills the kelp and thereby destroys the hiding places, the spawning grounds, and the spawn of fish; and that it also exposes shores to the destructive action of storms. Pro-

prietors of seaside resorts complain that the kelp set adrift by harvesters litters the beaches, temporarily ruining them for bathing. Great quantities of buoyant kelp are often set adrift by harvesters and come in on the beaches, whereas, if not cut, most of it would eventually sink. However, this littering of the beaches is periodic—less than the usual amount of sloughing occurring between cuts—and the perishable harvest drift is not so persistent as litter as the large plants which often are torn loose and washed up on the beaches; furthermore, this objection can be overcome by properly timing the cutting of beds adjacent to beach resorts.

It is not at all unlikely that clearing away the mat of kelp from the surface repeatedly would disturb the fish that hide in the shadows of it, and might drive away some. Doubtless the kelp indirectly furnishes some food to useful fish, as well as to some forms which are not useful. But harvesting does not destroy fish or fish spawn. Inspection of nearly 1,000 tons of kelp in process of being harvested and of hundreds of tons aboard the harvesters failed to reveal a total of 10 pounds of sea food, even including kelp crabs. Nor has careful examination, from rowboats, of hundreds of acres of kelp revealed a single fish egg.

Instead of its killing the kelp, harvesting is apparently beneficial to Macrocystis in many cases. It might thin out elk kelp (Pelagophycus) which grows and fruits at the top and which can not come up again from the base if cut off, but in the case of Macrocystis, which, normally is continuously renewing itself from the base, harvesting is comparable to pruning trees or cutting hay. Just as trees with very heavy foliage are sometimes uprooted in violent storms, so kelp plants with an excess of floating material are driven ashore in storms. Harvesting this floating material whenever a considerable quantity accumulates tends to reduce destruction of the beds by storms.

As for exposing the shores, the heavy "ground swell" seems able to get through any kelp bed, no matter how heavy, violent storms tearing out any plants that may oppose. In addition to maintaining a proper balance between holdfast and floating fronds, harvesting removes old fronds fouled with animal and vegetable growths, which obstruct the passage of light and are of little or no service to the plant. Usually in a heavy kelp mat there are uprooted plants drifting and decaying on the surface of the water along with rubbish of all kinds. Such refuse obstructs the passage of light, hinders circulation, and furnishes a breeding ground for disease. Harvesting clears this refuse away and floods with light the actively growing parts at the bases of the plants, stimulating the production of an abundant healthy new growth, and probably increasing the production of spores and the growth of new plants. On the other hand, most of the floating kelp usually consists of growing or recently matured fronds, which are absolutely necessary to the plants in elaborating their food materials; therefore, harvesting does injury in removing such fronds. Successive cutting, must, accordingly, be separated by sufficiently long intervals to allow the plants to renew their food supply. Furthermore, careless operation of a harvester, or the employment of improper methods, may result in the destruction of many plants, and should be guarded against.

GENERAL SUMMARY.

Kelp grows only where it has good anchorage.

The most favorable depth of water is 40 or 50 feet.

A temperature above 25° C. destroys Macrocystis.

Winds, currents, and waves favor growth.

Storms often tear out many plants.

The heaviest mats of kelp are seen late in autumn and again in spring. Fruit is most abundant in winter.

Macrocystis branches by the splitting of its leaves. A frond lives 4 to 7 months. A new frond grows up when an old one perishes.

Kelp may die and disappear suddenly when conditions are very unfavorable for growth. It may disappear gradually under less adverse conditions.

Black rot is the most important natural destroyer of kelp. Where no cutting is done, it destroys many floating fronds in warm, calm weather. Harvesting apparently controls the disease.

Harvesting destroys no fish spawn. Macrocystis benefits by thorough cutting through periods of two to four weeks, at intervals of three or four months.

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